ULTRAVIOLET REFLECTANCE PATTERNS IN THE ASTERACEAE, I. LOCAL AND CULTIVATED SPECIES[1].

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INTRODUCTION

This paper initiates a series that will survey ultraviolet reflectance patterns in the family Asteraceae. The first report of this phenomenon known to us for any plant family was made by Knuth (1891). Since the original study, numerous other workers, including Richtmyer (1923), Lutz (1924), Kugler (1929, 1941, 1947, 1951, 1955, 1963), Lotmar (1933), Seybold & Weissweiler (1944), Ziegenspeck (1955), Kullenberg (1956, 1961), Daumer (1956, 1958), Mazokhin-Porshnyakov (1959, 1969), Thomas & Autrum (1965), von Frisch (1967), Eisner *et al* (1969, 1972), Ornduff & Mosquin (1970), Thien (1971), Horovitz & Cohen (1972), Cruden (1972a, 1972b), and Watt *et al* (1974) have contributed to our knowledge of this important component of flower color.

Ultraviolet reflectance and absorption properties are usually invisible to man but are readily discernible to certain species of insects. Most of our knowledge of insect vision is based on the common honey bee (*Apis mellifera* L.), which has a visual capacity to see into the near ultraviolet region of the spectrum, *i.e.*, 250-400 nanometers (Thomas & Autrum, 1965). The patterns produced by UV reflection and UV absorption often indicate nectaries. Visible patterns of this type have been called nectar guides and were first reported by Sprengel in 1793.

As pointed out by Ornduff & Mosquin (1970), ultraviolet spectral characteristics can provide a special insight into evolutionary patterns that would not be evident using more classical methods. The family Asteraceae is especially appropriate for the present study because of its great abundance, the

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vast number of taxa (both in genera and species), and the extreme variation in their floral and capitulum morphology. We hasten to add that UV reflectance properties are but another characteristic of the taxon involved. Its use as a taxonomic tool should be kept in perspective.

Materials and methods. Complete inflorescences, single heads and habits of living plants were photographed in open sunshine and again with a visible-light absorbing filter (Kodak Wratten No 18A) which produces a picture based only on the ultraviolet reflectance properties of the flower.

Both Kodak Plus-X and Tri-X panchromatic films were used, both being sensitive to the 300-400 nm wave lengths that can be transmitted through the filter (Kodak Data Book, M-27). We used a lens of normal optical glass which absorbs all wave lengths of less than 350 nm (Rolls, 1968). Therefore, recorded patterns are restricted to the near ultraviolet region of the spectrum (between 350-400 nm). This span of wave lengths coincides very closely to the assumed peak sensitivity of ca. 350 nm for honey bees (Thomas & Autrum, 1965).

Results. The list of species examined (Table 1.) follows the tribal and subtribal arrangement of Hoffmann (1894). The genera of the Eupatorieae follow the concepts established by King and Robinson (1970a, 1970b, 1970c, 1970d) and the genera of the Senecioneae follow the concepts established by Robinson and Brettell (1973) and Robinson (1974). Collection numbers are those of the authors and the vouchers are deposited in the United States National Herbarium (US).

VERNONIEAE. Our observations of Vernonia novaboracensis and Elephantopus carolinianus are first reports for this tribe. V. novaboracensis was particularly interesting in that its marginal or outer disc flowers were ultraviolet reflecting. Heads of this species when mature often tend to become rather lax. Thus, the UV reflectance of the outer disc flowers and the nonreflectance of the inner disc flowers produces what we would call a "target" effect that is perhaps useful to some insects.

EUPATORIEAE. Two species in this tribe, Eupatorium cannabinum (Daumer, 1958, Kugler, 1963) and Liatris punctata (reported in the genus Laciniaria, Richtmyer, 1923) have previously been investigated. The report of non-UV reflectance in E. cannabinum agrees with our observations of other taxa in this tribe (Table I). Richtmyer reported strong UV reflectance in L. punctata.

The heads of most species in this tribe, even when mature, tend to remain tight or compact and, thus, it is unlikely that they will exhibit any "target" effect.

The genera Eupatoriadelphus, Conoclinium, Ageratum, Ageratina, and Mikania are reported here for the first time with regard to thir UV reflectance patterns.

Table 1. List of species examined.

Name	Voucher	Visible flower color		UV Reflectance	
		disc	ray	disc	ray
Vernonieae					
Vernonia noveboracensis (L.) Willd.	24, Potomac, Md.	purple	n/a	low at periphery	n/a
Elephantopus carolinianus Willd.	14, Potomac, Md.	purple	n/a	absent	n/a
Eupatorieae					
Eupatoriadelphus fistulosus (Barratt) King & H.Robinson	1, Rosslyn, Va.	reddish-purple	n/a	absent	n/a
Eupatoriadelphus fistulosus (Barratt) King & H.Robinson	39, Silver Spring, Md.	reddish-purple	n/a	absent	n/a
Eupatorium hyssopifolium L.	9, Silver Spring, Md.	white	n/a	absent	n/a
Eupatorium hyssopifolium L.	36, Silver Spring, Md.	white	n/a	absent	n/a
Eupatorium perfoliatum L.	61, Potomac, Md.	greyish-white	n/a	absent	n/a

Conoclinium coelestinum (L.) Cass.	13, Potomac, Md.	white	n/a	absent	n/a
Conoclinium coelestinum (L.) Cass.	28, Potomac, Md.	blue	n/a	absent	n/a
Ageratum houstonianum Miller	93, Washington, D.C.	blue	n/a	absent	n/a
Ageratina altissima (L.) King & H.Robinson	30, Potomac, Md.	greyish-white	n/a	absent	n/a
Mikania scandens L.	57, Thurmont, Md.	greyish-white	n/a	absent	n/a
Astereae					
Chrysopsis cf. mariana (L.) Ell.	23, Potomac, Md.	yellow	yellow	weak	weak
Solidago cf. caesia L.	60, Thurmont, Md.	yellow	yellow	absent	moderate
Solidago cf. canadensis L.	2, Rosslyn, Va.	yellow	yellow	absent	absent
Solidago cf. canadensis L.	35, Silver Spring, Md.	yellow	yellow	absent	absent
Solidago graminifolia (L.) Salisb.	38, Silver Spring, Md.	yellow	yellow	absent	absent

Solidago nemoralis Ait.	37, Silver Spring, Md.	yellow	yellow	absent	absent
Aster cf. cordifolius L.	59, Thurmont, Md.	yellow	blue or purple	very weak	weak
Aster cf. divaricatus L.	58, Thurmont, Md.	yellow	white	very weak	weak
Aster cf. ericoides L.	18, Potomac, Md.	yellow	white	absent	absent
Aster cf. lateriflorus (L.) Britt.	52, Thurmont, Md.	yellow	white or purplish	absent	absent
Aster cf. novae-angliae L.	67, Potomac, Md.	yellow	reddish-purple	absent	high
Aster cf. simplex Willd.	51, Thurmont, Md.	yellow	blue	absent	absent
Aster cf. simplex Willd.	54, Thurmont, Md.	yellow	white	absent	absent
Aster cf. simplex Willd.	55, Thurmont, Md.	yellow	blue	weak	weak
Aster cf. simplex Willd.	74, Frederick, Md.	yellow	bluish-white	very low	very low
Aster cf. simplex Willd.	76, Frederick, Md.	yellow	white	absent	absent
Conyza cf. canadensis (L.) Cronq.	5, Rosslyn, Va.	yellow	white or bluish	absent	absent

Conyza cf. canadensis (L.) Cronq.	20, Potomac, Md.	yellow	white	absent	absent
Erigeron cf. annuus (L.) Pers.	56, Thurmont, Md.	yellow	white	absent	absent
Erigeron cf. annuus (L.) Pers.	75, Thurmont, Md.	yellow	white	absent	absent
Erigeron sp.	53, Thurmont, Md.	yellow	white	absent	absent
Inuleae					
Gnaphalium obtusifolium, L.	72, Potomac, Md.	yellowish-white	n/a	absent	n/a
Heliantheae					
Polymnia uvedalia L.	4, Rosslyn, Va.	dark yellow or brown	yellow	absent	high upper half
Polymnia uvedalia L.	41, Rosslyn, Va.	dark yellow or brown	yellow	absent	high upper half
Ambrosia trifida L.	69, Potomac, Md.	yellowish	n/a	absent	n/a
Ambrosia trifida L.	70, Potomac, Md.	yellowish	n/a	absent	n/a
Ambrosia trifida L.	83, Washington D.C.	yellowish	n/a	absent	n/a

Zinnia elegans Jacq.	86, Potomac, Md.	yellowish	red-purple	absent	absent
Zinnia elegans Jacq.	87, Potomac, Md.	yellowish	yellow	absent	absent
Rudbeckia hirta L.	33, Potomac, Md.	dark brown	yellow	low	high, upper half
Rudbeckia hirta L.	85, Potomac, Md.	dark brown	yellow	low	high, upper half
Rudbeckia triloba L.	6, Silver Spring, Md.	dark brown	orange-yellow	very low	high, upper third
Rudbeckia triloba L.	73, Frederick, Md.	dark brown	orange-yellow	very low	high, upper third
Tithonia rotundifolia[2] (Miller) Blake	47, Washington, D.C.	yellow	reddish-orange	very low	very low upper half
Helianthus annuus L.[2]	92, Washington, D.C.	brownish	yellow	low	high, upper half
Helianthus strumosus L.	25, Potomac, Md.	brownish-yellow	yellow	absent	high, upper half
Helianthus tuberosus L.	42, Rosslyn, Va.	brownish-yellow	yellow	low or absent	high, upper half
Helianthus sp.	46, Washington, D.C.	dark brown	yellow	absent	high, upper half

Helianthus sp.	91, Washington, D.C.	brownish	yellow	very low	high, upper half
Verbesina alternifolia (L.) Britt.	15, Potomac, Md.	brown or green	yellow	absent	high, throughout
Verbesina alternifolia (L.) Britt.	64, Glen Echo, Md.	brown or green	yellow	absent	high, throughout
Verbesina occidentalis (L.) Walt.	63, Glen Echo, Md.	dark yellow or orange	yellow	absent	absent
Dahlia coccinea Cav.[2]	90, Washington, D.C.	yellow	red-purple	very low	very low
Bidens bipinnata L.	44, Rosslyn, Va.	yellow	n/a	absent	absent
Bidens frondosa L.	21, Potomac, Md.	orange or yellow	n/a	absent	very low
Bidens polylepis Blake	12, Potomac, Md.	dark yellow	yellow	weak	high, upper half
Cosmos sulphureus Cav.[2]	89, Washington, D.C.	dark yellow	red-orange	weak	absent
Galinsoga ciliata (Raf.) Blake	88, Washington, D.C.	yellow	white or pink	absent	absent
Tagetes erecta L.[2]	78, Washington, D.C.	yellow-orange	yellow-orange	absent	absent

Tagetes erecta L.[2]	80, Washington, D.C.	yellow-orange	yellow-orange	very low	very low
Tagetes patula L.[2]	79, Washington, D.C.	yellow	yellow	very low or absent	very low or absent
Tagetes patula L.[2]	81, Washington, D.C.	orange	orange	very low or absent	very low or absent
Tagetes patula L.[2]	82, Washington, D.C.	yellow-orange	orange-red	low or absent	low or absent
Anthemideae					
Achillea millefolium L.[1]	19, Potomac, Md.	white?	white	absent	absent
Chrysanthemum leucanthemum[1] L.	10, Silver Spring, Md.	yellow or brown	white	very low	absent
Chrysanthemum morifolium[2] Ramat.	48, Silver Spring, Md.	yellow	yellow	very low or absent	very low or absent
Chrysanthemum morifolium[2] Ramat.	49, Silver Spring, Md.	white	white	very low or absent	high at periphery
Chrysanthemum parthenium[1] (L.) Bernh.	68, Potomac, Md.	yellowish	white	very low or absent	absent
Chrysanthemum sp.	84, Potomac, Md.	pale yellow	pale yellow	very low or absent	absent

Artemisia vulgaris L.[1]	43, Rosslyn, Va.	purplish?	n/a	absent	n/a
Senecioneae					
Erechites hieracifolia (L.) Raf.	22, Potomac, Md.	yellow-white	n/a	absent	n/a
Arnoglossum atriplicifolia (L.) H. Robinson	26, Potomac, Md.	gray-white	n/a	absent	n/a
Cynareae					
Cirsium arvense (L.) Scop.	50, Washington, D.C.	pink-purple	n/a	absent	n/a
Cirsium altissimum (L.) Spreng.	3, Rosslyn, Va.	pink-purple	n/a	absent	n/a
Cirsium altissimum (L.) Spreng.	45, Rosslyn, Va.	pink-purple	n/a	absent	n/a
Cirsium discolor (Muhl.) Spreng.	17, Potomac, Md.	pink-purple	n/a	absent	n/a
Cirsium vulgare[1] (Savi.) Tenors	7, Rosslyn, Va.	pink-purple	n/a	absent	n/a
Centaurea cyanus L.[2]	94, Silver Spring, Md.	blue	n/a	high, at periphery	n/a

Centaurea nigrescens[1] Willd.	71, Potomac, Md.	purple	n/a	high, at periphery	n/a
Cichorieae					
Cichorium intybus L.[1]	8, Silver Spring, Md.	n/a	blue	n/a	high, at periphery
Taraxacum officinale[1] Wigg.	11, Silver Spring, Md.	n/a	yellow	n/a	high, at periphery
Sonchus asper (L.)[1] Hill	66, Glen Echo, Md.	n/a	yellow	n/a	high, at periphery
Sonchus oleraceus L.[1]	40, Silver Spring, Md.	n/a	yellow	n/a	high, at periphery
Sonchus uliginosus Bieb.[1]	62, Glen Echo, Md.	n/a	orange-yellow	n/a	high, at periphery
Lactuca sativa L.[2]	77, Frederick, Md.	n/a	yellow	n/a	absent
Lactuca scariola L. var. integrata Gren. & Godr.[1]	65, Glen Echo, Md.	n/a	yellow	n/a	absent
Hieracium gronovii L.	16, Potomac, Md.	n/a	yellow	n/a	high, at periphery

[1]Naturalized
[2]Cultivated
n/a Not Applicable

ASTEREAE. UV reflectance patterns for five species in five genera have previously been reported for this tribe. All reports indicated that the disc flowers were UV absorbing. The ray flowers of Bellis perennis, Boltonia latisquama (Kugler, 1963), and Grindelia squarrosa (Richtmyer, 1923) were reported as being only weakly UV reflective. All flowers of Aster linosyris (Kugler, 1963) and Solidago missouriensis (Richtmyer, 1923) were completely UV absorbing.

Aster cf. novae-angliae is very exceptional. In visible light this species has reddish-purple ray flowers and yellow disc flowers. Its ray flowers showed a high degree of UV reflectance and the disc flowers were UV absorbing (Figure 24).

Our investigations of Chrysopsis, Conyza and Erigeron constitute first reports for these genera.

INULEAE. The UV reflectance patterns for three species in this tribe have been previously reported (Kugler, 1963). Buphthalmum salicifolium showed UV reflectance in distal portion of the ligule of its ray flowers. Helichrysum bracteatum was totally nonreflecting and the ray flowers of Inula ensifolia were UV reflecting throughout.

Most of the genera and species of this tribe have very small, inconspicuous flowers which are often nearly completely enclosed by phyllaries. One notable exception seems to be some species in the genus Inula which often have conspicuous ligules. These ligules make possible a "target" effect and Kugler's report seems to confirm this.

Our report of Gnaphalium obtusifolium is a first report for the genus.

HELIANTHEAE. Our studies of UV reflectance in this tribe basically agree with those of other workers that are summarized in Table 2. The flowers of Ambrosia trifida were completely UV absorbing, not surprising in that the genus is only wind-pollinated. Our reports of the UV reflectance patterns for Bidens, Cosmos, Dahlia, Galinsoga, Polymnia, Tithonia, and Verbesina (Table 1) are first reports for these genera.

ANTHEMIDEAE. Our report for Achillea millefolium (Table 1) agrees with that of Kugler (1965). All previous reports for species of Chrysanthemum (Kugler, 1963) indicate no UV reflectance patterns. However, one of the white-flowered horticultural forms of C. morifolium, which we photographed, showed high UV reflectance in its peripheral ray flowers. A yellow-flowered form of the same species showed very low or no UV reflectance. This is surprising in that we would have expected exactly the opposite situation.

Artemisia vulgaris is a first report for the genus.

Table 2. Species of Heliantheae previously reported.

Name	Reflectance Patterns	Reference
Bidens mitis Sherff	upper half of ray flowers reflective	Eisner et al, 1969
Coreopsis sp.	absent, totally non-reflecting	Kugler, 1963
Coreopsis bicolor Bossee	upper half of ray flowers reflective	Daumer, 1958
Coreopsis leavenworthii Torrey & Gray	both ray and disc flowers non-reflective	Eisner et al, 1969
Cosmos bipinnatus Cav.	non-reflective	Daumer, 1958
Dahlia scapigera Knowles and Westc.	non-reflective	Lotmar, 1933
Gaillardia maxima Gray	upper half of ray flowers reflective	Daumer, 1958
Helenium autumnale L.	upper half of ray flowers reflective	Daumer, 1958
Helenium tenuifolium Nutt.	ray flowers reflective, disc flowers non-reflective	Eisner et al, 1969
Helianthus annuus L.	upper half of ray flowers strongly UV reflective	Kugler, 1963 Richtmyer, 1923
Helianthus annuus L.	upper half of ray flowers reflective	Daumer, 1958
Helianthus annuus L.	disc flowers & basal portion of ray flowers non-reflective	Lotmar, 1933
Helianthus rigidus (Cass.) Desf.	upper half of ray flowers reflective	Daumer, 1958
Helianthus strumosus L.	upper half of ray flowers strongly UV reflective	Kugler, 1963

Table 2. (continued)

Helianthus (cultivated)	apparently was completely UV absorbing	Richtmyer, 1923
Heliopsis laevis Pers.	upper half of ray flowers reflective	Daumer, 1958
Laya elegans Torr. & Gray	absent, totally non-reflective	Kugler, 1963
Ratibida columnaris Raf.	some?	Richtmyer, 1923
Rudbeckia sp.	disc flowers & basal portions of ray flowers non-reflective	Eisner et al, 1969
Rudbeckia deamii Blake	upper half of ray flowers strongly UV reflective	Kugler, 1963
Rudbeckia hirta L.	upper half of ray flowers reflective	Daumer, 1958
Rudbeckia hirta L.	upper half of ray flowers strongly UV reflective	Thompson, Meinwald, Aneshansley and Eisner, 1972
Rudbeckia hirta L.	upper half of ray flowers strongly UV reflective	Eisner, Eisner, Hyypio, Aneshansley & Silberglied, 1972
Rudbeckia laciniata L.	some, not specified where, however	Richtmyer, 1923
Rudbeckia newmani Loud.	upper half of ray flowers strongly UV reflective	Kugler, 1963
Sanvitalia procumbens Lam.	apical tips of ray flowers UV reflective	Kugler, 1963
Tagetes patula L.	absent, totally non-reflective	Daumer, 1958
Tagetes signatus Bartl.	absent, totally non-flective	Kugler, 1963

Viguiera dentata	disc flowers and lower ¼ of ray flowers non-reflective	Eisner et al, 1969
Zinnia haageana Rgl.	apical portions of ray flowers UV reflective	Kugler, 1963

SENECIONEAE. Kugler (1963) has reported the following radiate species, Doronicum pardalianches L., Senecio cordatus Koch, Senecio fuchsii Gmelin, Senecio jacobaea L., and Tussilago farfara Tod. as having ray flowers that strongly reflect UV wave length. He further indicates that the rayless species, Emilia sonchifolia DC and Petasites albus (L.) Gaertn, are UV absorbing. Our reports of Erechites hieracifolia (L.) Raf. and Arnoglossum atriplicifolia (L.) H. Robinson are first reports for the genera and were totally nonreflecting.

CYNAREAE. All taxa in this tribe which have been investigated have been completely UV absorbing except for two species of Centaurea. C. Cyanus was reported by Kugler (1963) as having some UV reflectance in its outer disc flowers. Our photograph of C. nigrescens shows a similar pattern (Fig. 110). Both species have heads which are rather lax and present a flat-topped appearance giving a target effect.

CICHORIEAE. Our reports in Table 1. of UV reflexance in this tribe agree with those previously published except for Cichorium intybus L. (Table 3). Kugler (1963) reports this species as being totally nonreflective. Our picture of C. intybus (Fig. 112) disagrees with his report and shows considerable UV reflectance in the marginal ray flowers.

Our reports for Sonchus, Lactuca and Hieracium are first reports for these genera.

ARCTOTIDEAE. Kugler (1963) has reported patterns for three species in this tribe. Arctotis calendulacea and A. stoechadifolia reflect UV radiation in the apical region of their ray flowers. Gazania splendens has been reported as having a small spot at the base of its ray flowers which is UV reflecting. No species of this tribe are reported in the present paper.

CALENDULEAE. Daumer (1958) has reported Calendula officinalis L. as being nonreflective.

Table 3. Species of Cichorieae previously reported.

Name	Reflectance Patterns	Reference
Aposeris foetida (L.) Less.	apical parts of ray flowers reflect throughout flower	Kugler, 1963
Catananche caerulea L.	absent, totally non-reflecting	Kugler, 1963
Cichorium intybus L.	absent, totally non-reflecting	Kugler, 1958, 1963
Crepis biennis L.	apical regions of marginal ray flowers reflect	Kugler, 1963
Hieracium murorum L.	marginal ray flowers reflect throughout	Kugler, 1963
Lampsana communis L.	apical regions of marginal ray flowers reflect	Kugler, 1963
Leontodon hastilis L.	apical regions of marginal ray flowers reflect	Kugler, 1963
Taraxacum officinale Weber	marginal ray flowers reflect throughout	Kugler, 1958, 1963
Tragopogon pratensis L.	marginal ray flowers reflect throughout	Kugler, 1963

DISCUSSION AND CONCLUSIONS

The family Asteraceae is composed of taxa which exhibit one of the three basic types of heads.

1. heads composed of only disc flowers
2. heads composed of both disc and ray flowers
3. heads composed of only ray flowers

In discoid genera and tribes composed of all or mostly discoid species such as the Vernonieae, Eupatorieae and Cynareae, the heads are usually nonreflective. However, in three species, Vernonia noveboracensis, Centaurea cyanus, and C. nigrescens, the marginal disc flowers were UV reflective and the inner disc flowers were UV absorbing. This reflectance may be associated with the age of the flowers in the head but in any event it produces what we would call a target effect.

In radiate genera and tribes composed of mostly species with both ray flowers and disc flowers such as the Asteraceae, Heliantheae and Senecioneae the heads often give a target effect. This is accomplished in the following ways.

1. The ray flowers may reflect UV throughout as in Aster cf. novae-angliae and Verbesina alternifolia.

2. Only the upper half of the ray flower reflects UV as in species of Helianthus and Rudbeckia.

3. Only the very apical portions of ray flowers may reflect UV as in Sanvitalia procumbens (Kugler, 1963).

In all of the above cases, the disc flowers were nonreflective and thus a target effect is produced.

The third basic type of head is characteristic of the Cichorieae tribe and presents a very interesting situation. All of its species have heads composed entirely of ray flowers. Yet these species often have heads which show very good target patterns. In the Cichorieae, this is accomplished in a number of ways.

1. The marginal ray flowers may be UV reflective throughout as in some species of Hieracium, Taraxacum and Tragopogon.

2. Only the apical region of the ray flowers may be UV reflective as in some species of Aposeris, Lampsana and Crepis.

Self-pollinating and apomictic species don't seem to "lose" their strongly defined ultraviolet patterns. This situation may parallel that found in some self-pollinating flowers that are large and showy, even though their usual role in attracting insects has long been abandoned.

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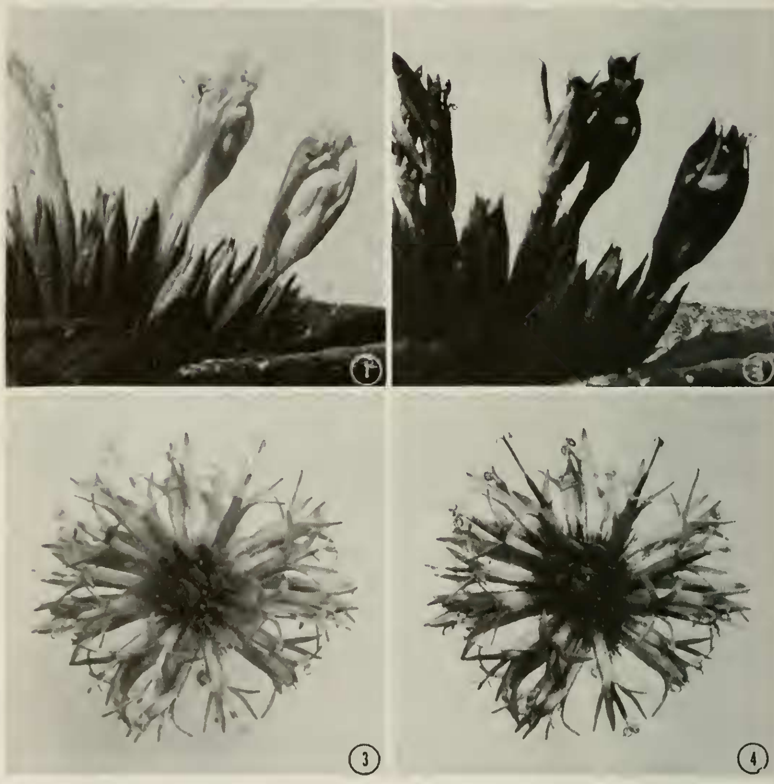

Plate 1, Figures 1-4. Vernonieae. Figures 1-2. Elephantopus carolinianus, head; 1. visible light; 2. ultraviolet. Figures 3-4. Vernonia noveboracensis, head; 3. visible light; 4. ultraviolet.

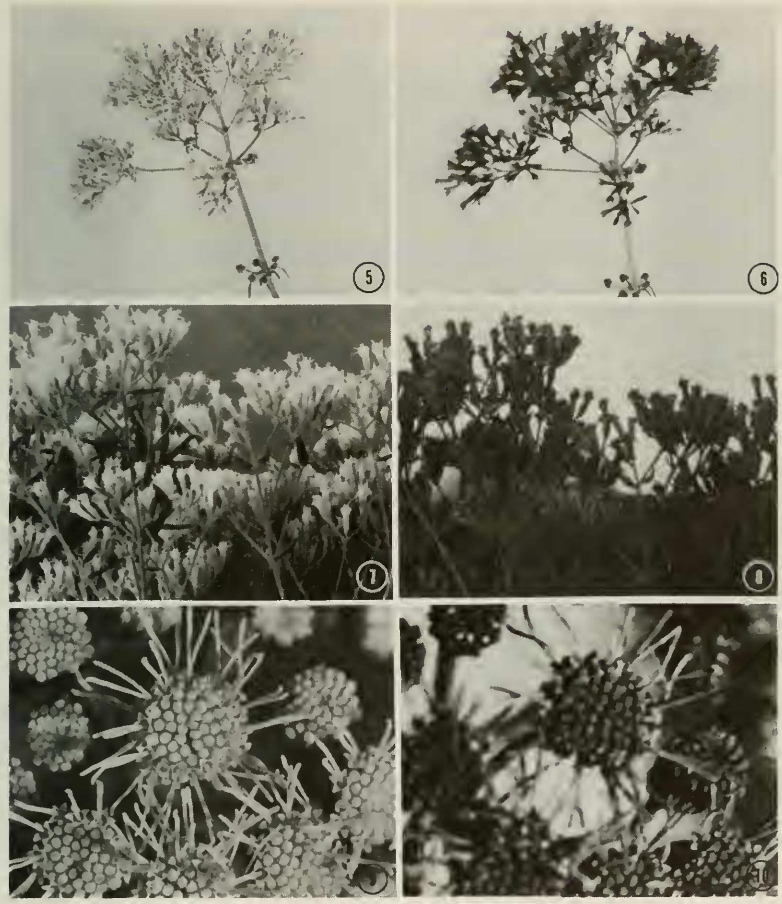

Plate 2, Figures 5-10. Eupatorieae. Figures 5-6. Eupatoriadelphus fistulosus, habit; 5. visible light; 6. ultraviolet. Figures 7-8. Eupatorium hyssopifolium, inflorescence; 7. visible light; 8. ultraviolet. Figures 9-10. Conoclinium coelestinum, heads; 9. visible light; 10. ultraviolet.

Plate 3, Figures 11-14. Eupatorieae. Figures 11-12. Eupatorium perfoliatum, habit; 11. visible light; 12. ultraviolet. Figures 13-14. Mikania scandens, habit; 13. visible light; 14. ultraviolet.

Plate 4, Figures 15-18. Eupatorieae-Astereae. Figures 15-16. Mikania scandens, inflorescence; 15. visible light; 16. ultraviolet. Figures 17-18. Solidago nemoratis, habit; 17. visible light; 18. ultraviolet.

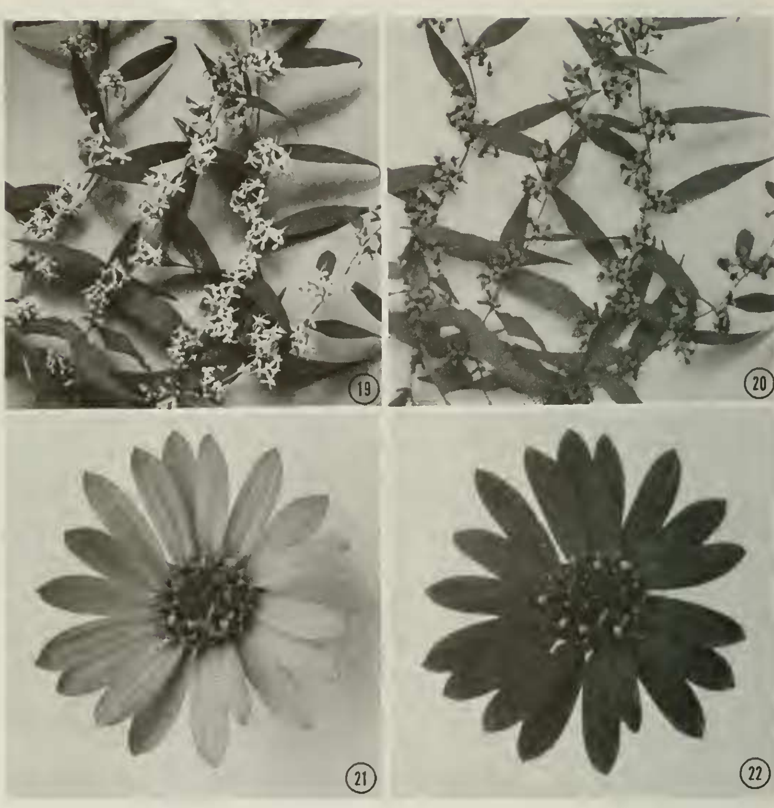

Plate 5, Figures 19-22. Astereae. Figures 19-20. Chrysopsis cf. mariana, head; 19. visible light; 20. ultraviolet. Figures 21-22. Solidago cf. caesia, habit; 21. visible light; 22. ultraviolet.

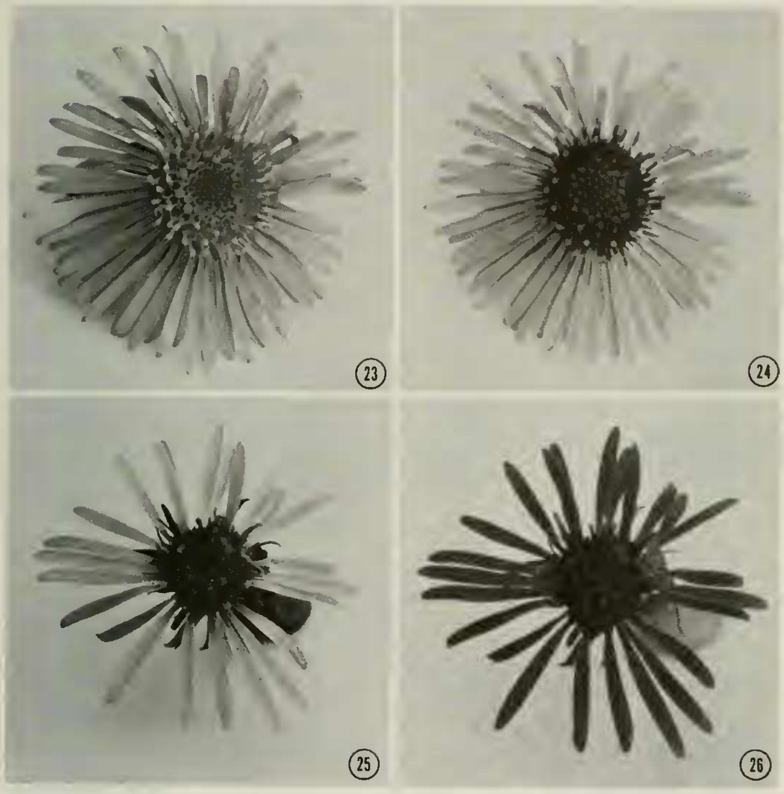

Plate 6, Figures 23-26. Astereae. Figures 23-24. Aster cf. novae-angliae, head; 23. visible light; 24. ultraviolet. Figures 25-26. Aster cf. simplex, head; 25. visible light; 26. ultraviolet.

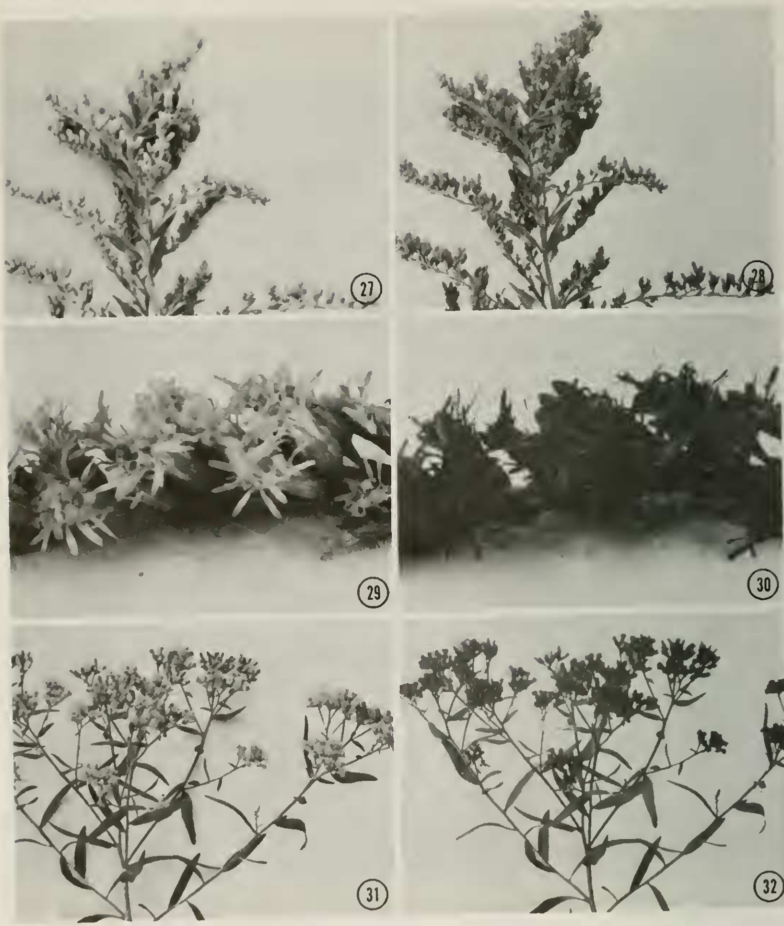

Plate 7, Figures 27-32. Astereae. Figures 27-28. Solidago cf. canadensis, habit; 27. visible light; 28. ultraviolet. Figures 29-30. Solidago cf. canadensis, inflorescence; 29. visible light; 30. ultraviolet. Figures 31-32. Solidago graminifolia, habit; 31. visible light; 32. ultraviolet.

Plate 8, Figures 33-36. Astereae. Figures 33-34. Solidago graminifolia, inflorescence; 33. visible light; 34. ultraviolet. Figures 35-36. Aster cf. divaricatus, habit; 35. visible light; 36. ultraviolet.

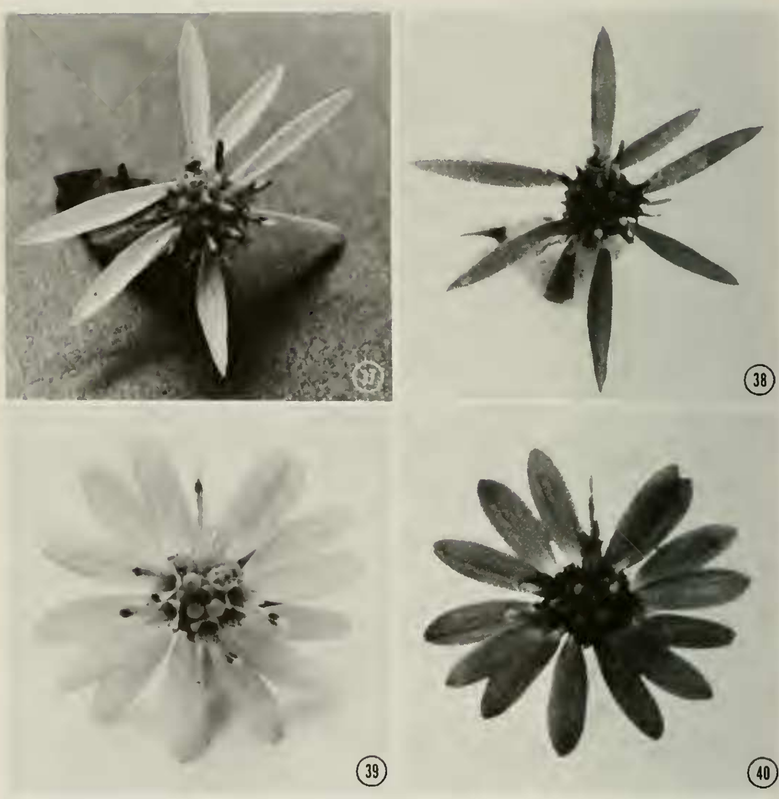

Plate 9, Figures 37-40. Astereae. Figures 37-38. Aster cf. divaricatus, head; 37. visible light; 38. ultraviolet. Figures 39-40. Aster cf. cordifolius, head; 39. visible light; 40. ultraviolet.

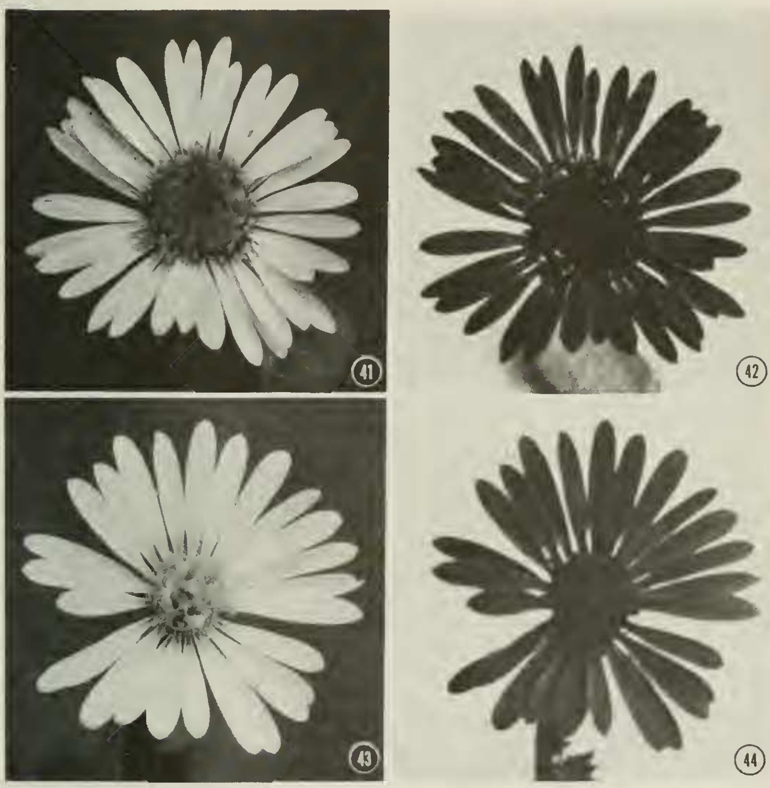

Plate 10, Figures 41-44. Astereae. Figures 41-42. Conyza cf. canadensis, head; 41. visible light; 42. ultraviolet. Figures 43-44. Aster cf. ericoides, head; 43. visible light; 44. ultraviolet.

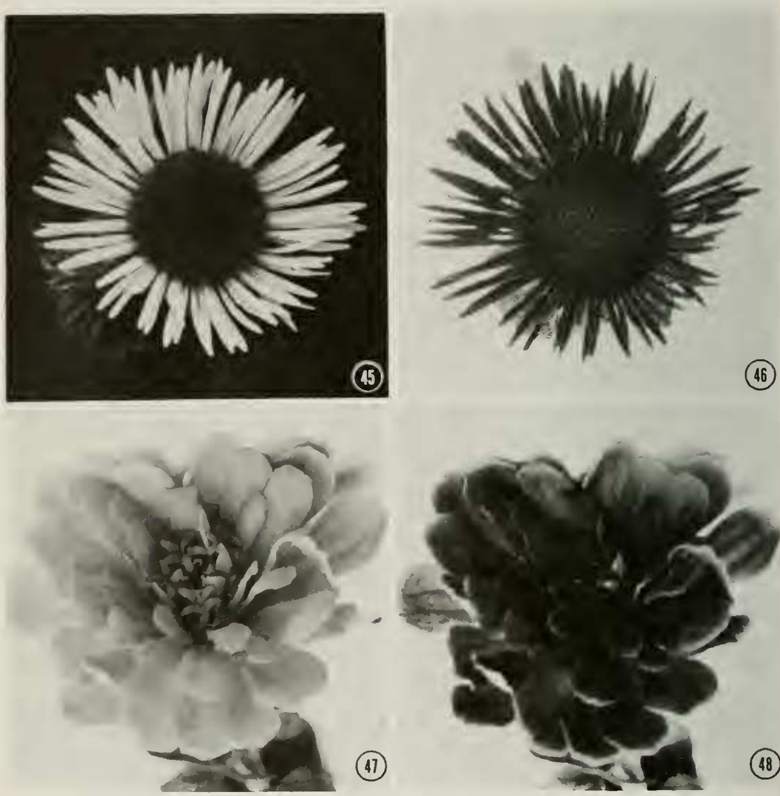

Plate 11, Figures 45-48. Astereae-Heliantheae. Figures 45-46. Erigeron cf. annuus, head; 45. visible light; 46. ultraviolet. Figures 47-48. Zinnia elegans, head; 47. visible light; 48. ultraviolet.

Plate 12, Figures 49-52. Heliantheae. Figures 49-50. Polymnia uvedalia, head; 49. visible light; 50. ultraviolet. Figures 51-52. Rudbeckia triloba, head; 51. visible light; 52. ultraviolet.

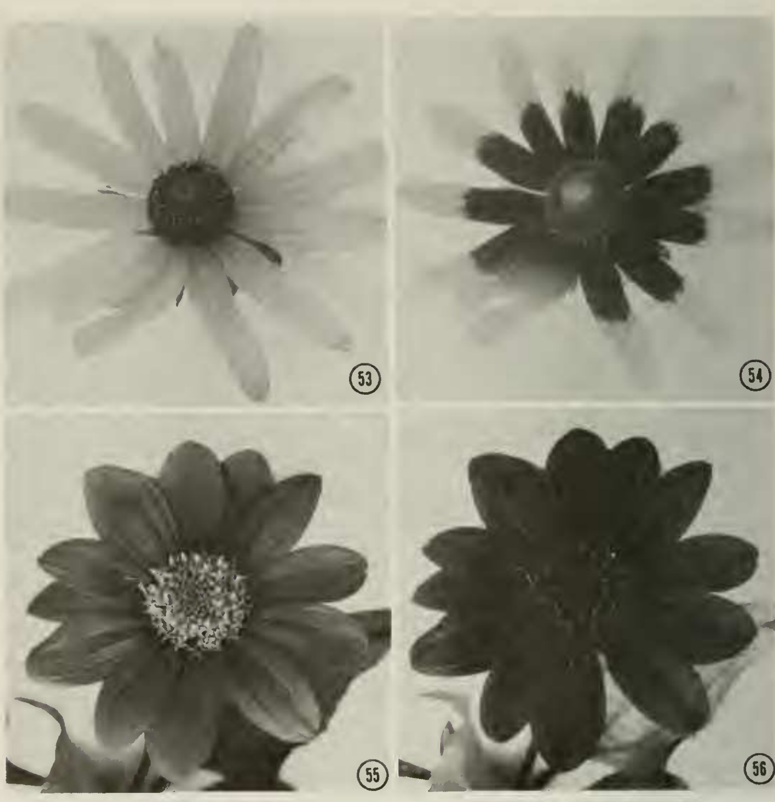

Plate 13, Figures 53-56. Heliantheae. Figures 53-54. Rudbeckia hirta, head; 53. visible light; 54. ultraviolet. Figures 55-56. Tithonia rotundifolia, head; 55. visible light; 56. ultraviolet.

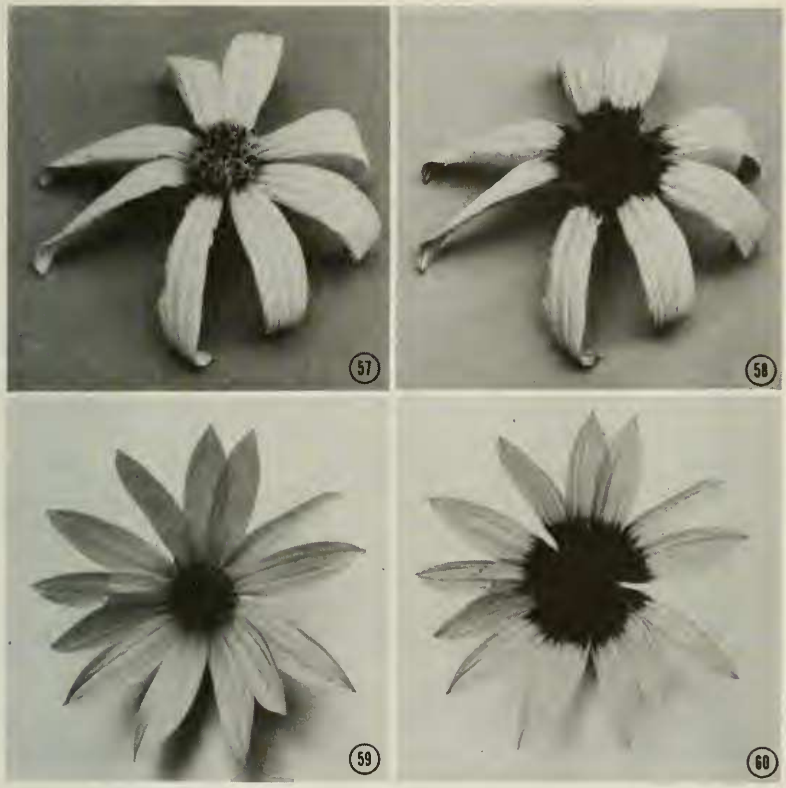

Plate 14, Figures 57-60. Heliantheae. Figures 57-58. Helianthus strumosus, head; 57. visible light; 58. ultraviolet. Figures 59-60. Helianthus tuberosus, head; 59. visible light; 60. ultraviolet.

Plate 15, Figures 61-64. Heliantheae. Figures 61-62. Helianthus sp., head; 61. visible light; 62. ultraviolet. Figures 63-64. Helianthus annuus, head; 63. visible light. 64. ultraviolet.

Plate 16, Figures 65-68. Heliantheae. Figures 65-66. Helianthus sp., head; 65. visible light. 66. ultraviolet. Figures 67-68. Verbesina alternifolia, head; 67. visible light. 68. ultraviolet.

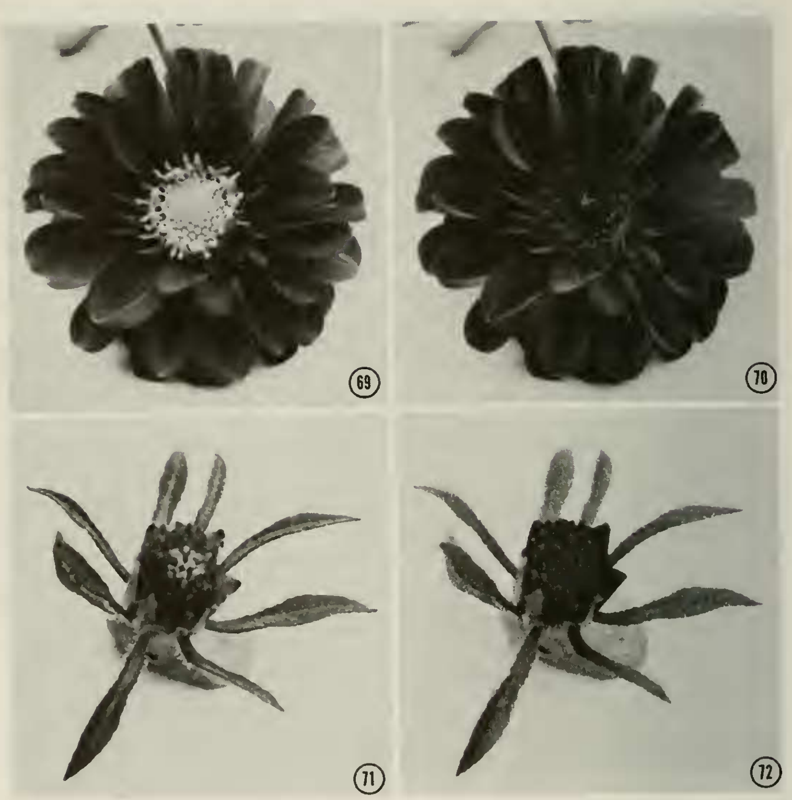

Plate 17, Figures 69-72. Heliantheae. Figures 69-70. Dahlia coccinea, head; 69. visible light. 70. ultraviolet. Figures 71-72. Bidens frondosa, head; 71. visible light; 72. ultraviolet.

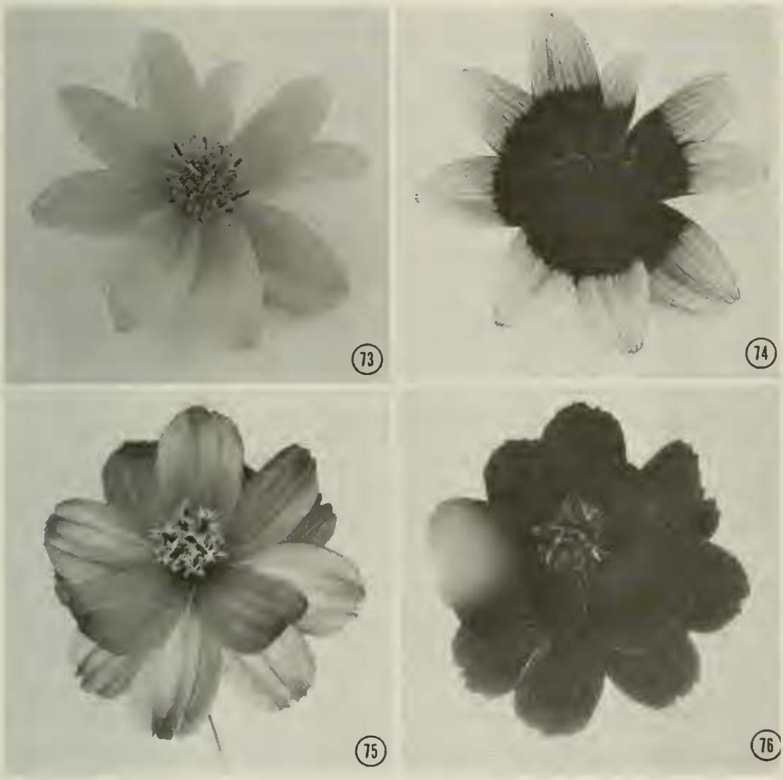

Plate 18, Figures 73-76. Heliantheae. Figures 73-74. Bidens polylepis, head; 73. visible light; 74. ultraviolet. Figures 75-76. Cosmos sulphureus, head; 75. visible light; 76. ultraviolet.

Plate 19, Figures 77-80. Heliantheae. Figures 77-78. Tagetes erecta, habit; 77. visible light; 78. ultraviolet. Figures 79-80. Tagetes erecta, head; 79. visible light; 80. ultraviolet.

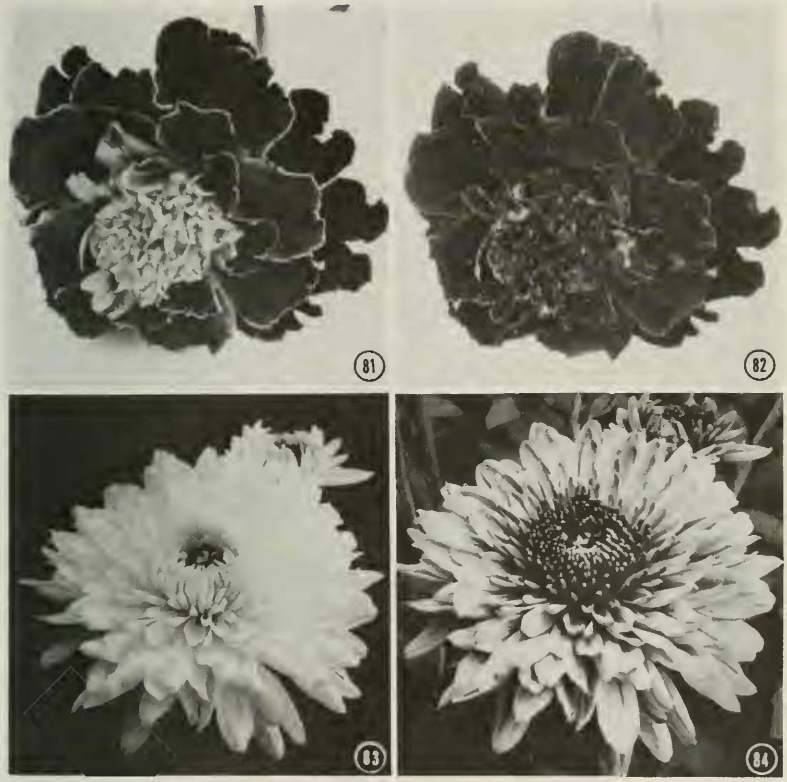

Plate 20, Figures 81-84. Heliantheae-Anthemideae. Figures 81-82. Tagetes patula, head; 81. visible light; 82. ultraviolet. Figures 83-84. Chrysanthemum morifolium, head; 83. visible light; 84. ultraviolet.

Plate 21, Figures 85-88. Anthemideae. Figures 85-86. Chrysanthemum morifolium, head; 85. visible light; 86. ultraviolet. Figures 87-88. Chrysanthemum parthenium, head; 87. visible light; 88. ultraviolet.

Plate 22, Figures 89-92. Anthemideae. Figures 89-90. Chrysanthemum parthenium, head; 89. visible light; 90. ultraviolet. Figures 91-92. Chrysanthemum sp., head; 91. visible light; 92. ultraviolet.

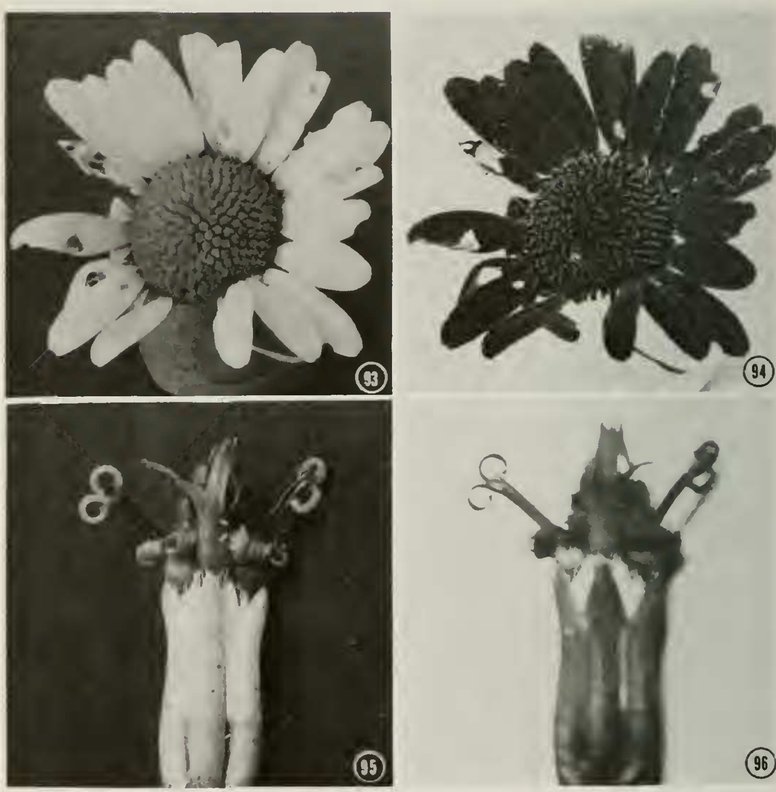

Plate 23, Figures 93-96. Anthemideae-Senecioneae. Figures 93-94. Chrysanthemum leucanthemum, head; 93. visible light; 94. ultraviolet. Figures 95-96. Arnoglossum atriplicifolia, head; 95. visible light; 96. ultraviolet.

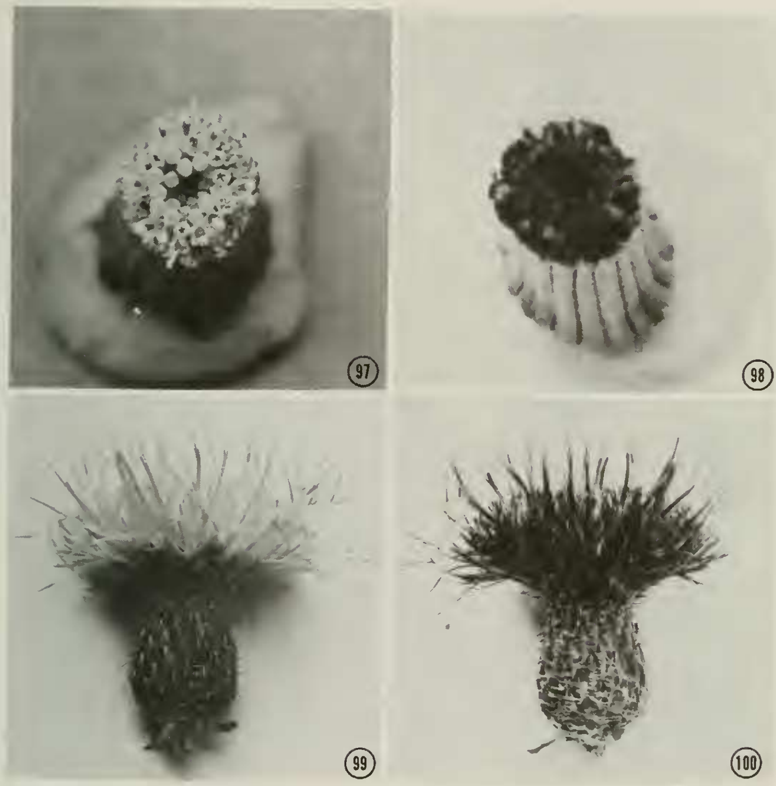

Plate 24, Figures 97-100. Senecioneae-Cynareae. Figures 97-98. Erechites hieracifolia, head; 97. visible light; 98. ultraviolet. Figures 99-100. Cirsium altissimum, head; 99. visible light; 100. ultraviolet.

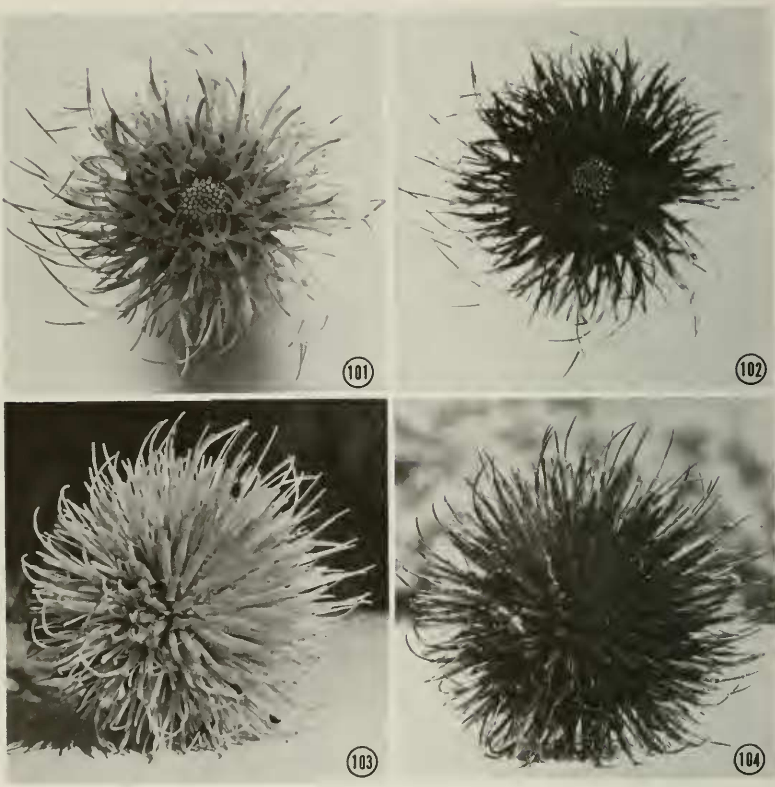

Plate 25, Figures 101-104. Cynareae. Figures 101-102. Cirsium altissimum, head; 101. visible light; 102. ultraviolet. Figures 103-104. Cirsium discolor, head; 103. visible light; 104. ultraviolet.

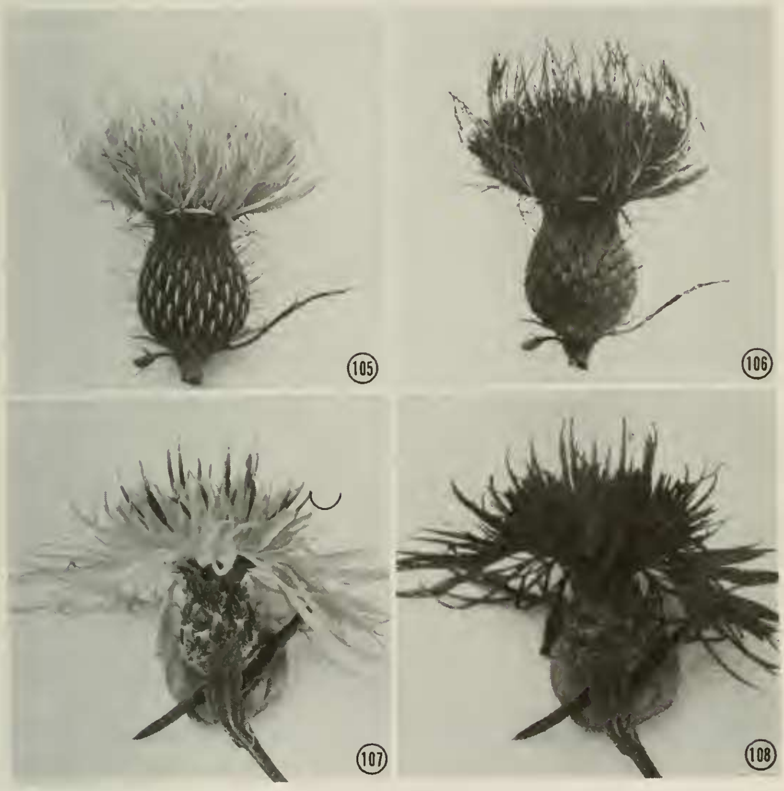

Plate 26, Figures 105-108. Cynareae. Figures 105-106. Cirsium vulgare, head; 105. visible light; 106. ultraviolet. Figures 107-108. Centaurea nigrescens, head; 107. visible light; 108. ultraviolet.

Plate 27, Figures 109-112. Cynareae-Cichorieae. Figures 109-110. Centaurea nigrescens, head; 109. visible light; 110. ultraviolet. Figures 111-112. Cichorium intybus, head; 111. visible light; 112. ultraviolet.

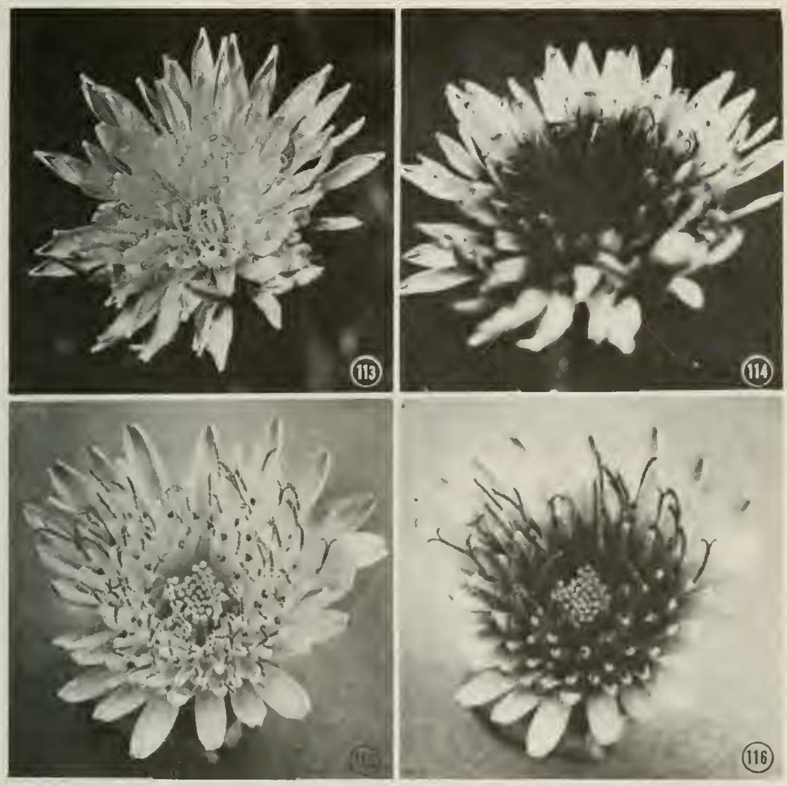

Plate 28, Figures 113-116. Cichorieae. Figures 113-114. Taraxacum officinale, head; 113. visible light; 114. ultraviolet. Figures 115-116. Sonchus oleraceus, head; 115. visible light; 116. ultraviolet.

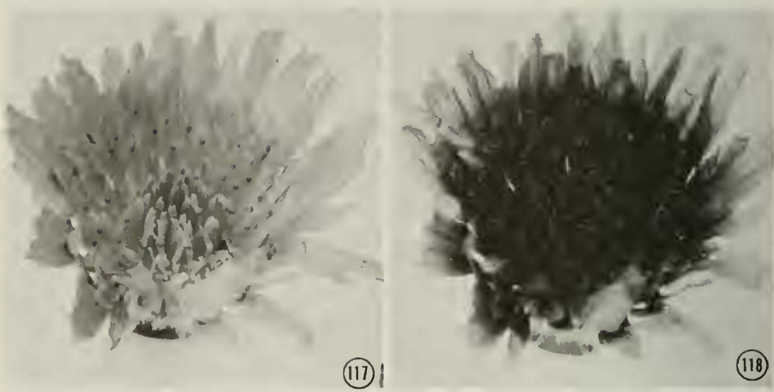

Plate 29, Figures 117-118. Cichorieae. Figures 117-118. Sonchus asper, head; 117. visible light; 118. ultraviolet.